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RESEARCH ARTICLE

Locomotor function after long-duration space flight: effects and motor learning during recovery

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Abstract Astronauts returning from space flight and performing Earth-bound activities must rapidly transition from the microgravity-adapted sensorimotor state to that of Earth's gravity. The goal of the current study was to assess locomotor dysfunction and recovery of function after long-duration space flight using a test of functional mobility. Eighteen International Space Station crewmembers experiencing an average flight duration of 185 days performed the functional mobility test (FMT) pre-flight and post-flight. To perform the FMT, subjects walked at a self selected pace through an obstacle course consisting of several pylons and obstacles set up on a base of 10-cm-thick, medium-density foam for a total of six trials per test session. The primary outcome measure was the time to complete the course (TCC, in seconds). To assess the long-term recovery trend of locomotor function after return from space flight, a multilevel exponential recovery model was fitted to the log-transformed TCC data. All crewmembers exhibited altered locomotor function after space flight, with a median 48% increase in the TCC. From the fitted model we calculated that a typical subject would recover to 95% of his/her pre-flight level at approximately 15 days post-flight. In addition, to assess the early motor learning responses after returning from space flight, we modeled performance over the six trials during the first post-flight session by a similar multilevel exponential relation. We found a significant positive correlation between measures of long-term recovery and early motor learning ($P < 0.001$) obtained from the respective models. We concluded that two types of recovery processes influence an astronaut's ability to re-adapt to Earth's gravity environment. Early motor learning helps astronauts make rapid modifications in their motor control strategies during the first hours after landing. Further, this early motor learning appears to reinforce the adaptive realignment, facilitating re-adaptation to Earth's 1-g environment on return from space flight.

Keywords Functional mobility · Space flight · Locomotion · Adaptation · Recovery

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Introduction

Exposure to the microgravity conditions of space flight induces adaptive modification in sensorimotor function. Upon return to Earth's 1-g environment, these modifications cause various disturbances in perception, spatial orientation, posture, gait, and eye–head coordination (Reschke et al. 1996; Bloomberg et al. 1997; Reschke et al. 1998; Bloomberg and Mulavara 2003; Courtine and Pozzo 2004). Early studies investigating the effects of space flight on locomotor control showed that after space flight, subjects tend to exhibit a stamping gait, drift off the intended path, raise their arms to the side frequently, take small irregularly spaced steps for greater stability, and adopt a wide base of support (Chekirda et al. 1971; Bryanov et al. 1976). More recent studies of changes in locomotor function after space flight have documented changes in speed while walking around corners (Glasauer et al. 1995), significant modifications in the spatial and temporal features of muscle activation and increased within-day activation variability (Layne et al. 1997, 1998, 2001, 2004), increased variability in ankle and knee joint motion (McDonald et al. 1996; Bloomberg and Mulavara 2003), alterations in head–trunk control (Bloomberg et al. 1997; Bloomberg and Mulavara 2003), and alterations in ability to coordinate effective landing strategies during jump tasks (Newman et al. 1997; Courtine and Pozzo 2004).

Astronauts returning from space flight and performing Earth-bound activities must rapidly transition from one sensorimotor state to another. For returning crewmembers, the rate of recovery of sensorimotor function varies, as crewmembers evoke different recovery mechanisms to re-adapt (Edgerton and Roy 1996; Boyle et al. 2001; Bloomberg and Mulavara 2003; Courtine and Pozzo 2004). Early Russian investigations studying the effects of 2–30 days of space flight on locomotor control showed that the post-flight performance decrements were related in most cases to the length of the flight and performance recovered, on average, within 2 days and in most cases within 2 weeks (Bryanov et al. 1976, cited in Clement and Reschke 2008). The magnitude and time course of balance control recovery during standing was investigated using a clinical posturography system (Equitest, Neurocom International) on astronauts returning from Space Shuttle missions ranging from 5 to 13 days (Paloski et al. 1992). These investigations found that the recovery time course followed a double exponential path with a rapid improvement in stability during the first 8–10 h followed by a more gradual return to pre-flight stability levels over the next 4–8 days. In a previous study we reported a reduction in compensatory head pitch movements during post-flight locomotion followed by a recovery trend spanning 6–10 days in crewmembers returning from missions to the MIR space station after 4–6 months (Bloomberg and Mulavara 2003). Courtine and Pozzo (2004) investigated the spatial and temporal patterns of head and trunk movements of cosmonauts walking over ground, ascending stairs, and jumping down from a platform after returning from space flight that lasted 6 months. They reported that 2 days after returning from long-duration space flight subjects held their heads at significantly lower positions in the pitch plane than pre-flight, but head stability did not change, and coordination patterns between head and trunk segments were not disrupted. Importantly, all the variables that showed gait disruptions had recovered to pre-flight levels by 6 days after their return from space flight.

The goal of this investigation was to assess locomotor dysfunction and recovery of function after long-duration space flight using a functional task that consists of traversing an obstacle-avoidance course. This functional mobility test (FMT) was designed to provide information on the functional implications of post-flight locomotor dysfunction. The primary outcome measure studied was the time to complete the course (TCC, in seconds). Here, we quantify subjects' recovery of performance and the learning processes involved during re-adaptation in functional mobility after long-duration space flight.

Methods

Subjects

Eighteen crewmembers taking part in long-duration missions aboard the International Space Station (ISS) ranging from 163 to 195 days volunteered to participate in this study. They included 17 males, 1 female, mean age 46 years (range 37–54 years). Fourteen subjects had prior space flight experience. All subjects gave informed consent according to the requirements of the Committee for the Protection of Human Subjects at NASA Johnson Space Center.

Functional mobility test

In the FMT, crewmembers were required to navigate an obstacle course set up on a base of 10-cm-thick, medium-density foam (Sunmate Foam, Dynamic Systems, Inc., Leicester, NC, USA), as shown in Fig. 1. The compliant foam changes continually as the individual stands on it, making the support surface unreliable. The foam was used to make proprioceptive information unreliable during ambulation. It had an added benefit for safety: if anyone had fallen it would have provided a soft landing. The 6.0 m × 4.0 m course consisted of the following obstacles: (1) five foam pylons arranged in a "slalom" fashion hung from the ceiling, which required the subject to change heading direction continuously, (2) a gate with edges defined using two foam pylons hung from the ceiling, the width of which was adjusted to the width of the crewmember's shoulders, so they had to walk between the pylons "sideways", (3) a 46-cm high Styrofoam block placed on the foam surface which forced the crewmember to balance on one foot on an unstable surface (foam) while clearing the obstacle, and (4) a "portal" constructed of two successive 31-cm high Styrofoam blocks placed on the foam surface, with a horizontal foam bar hung from the

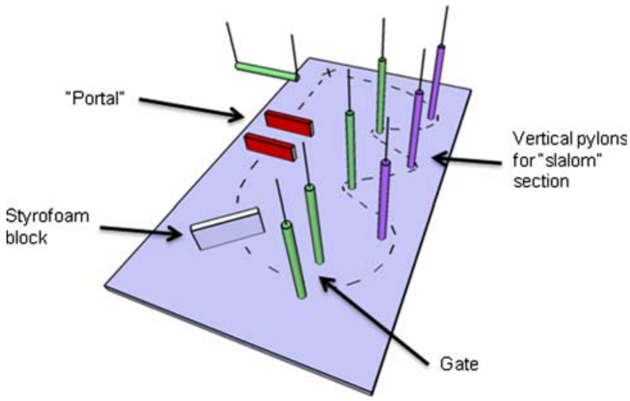

Fig. 1 Functional mobility test (FMT): obstacle course used to assess locomotor function in returning astronauts

ceiling between these blocks, the height of which was adjusted to that of the crewmember's shoulders requiring crewmembers to bend at the waist or lower themselves to avoid hitting the bar hung from the ceiling and balance on a single foot on a compliant surface while stepping over the barrier.

Sessions

Table 1 contains the different days on which the pre- and post-flight data were collected. Baseline FMT performance data reported here were collected during two pre-flight sessions occurring between 314 and 45 days before launch.

Table 1 Different days on which the pre- and post-flight data were collected

Subject No.	Pre-flight (days)		Post-flight (days)						
1	126	68	0	1		4	7	12	
2	126	68	0	1		4	6	11	
3	131	65	0	1		4	6	11	
4	149	45			2	4	7	12	46
5	151	45		1	2	4	7	12	
6	151	45		1	2	4	7	12	
7	162	128		1	2	4	7	24	
8		162		1	2	4	7	23	
9	75	50		1	2	3	7	25	
10	264	75		1	2	4	7	24	
11	59	51		1	2	3	6	24	
12	53	52		1	2	3	6	24	
13	126	62		1	2	4	7	24	
14	314	61		1	2	4	7	21	
15	142	72		1	2	4	7	23	
16	144	74		1	2	4	7	22	
17		80			2	4	7	22	
18	413	92		1	2	4	7	29	

Two subjects, however, participated in only one pre-flight session due to scheduling problems. Data were obtained from three crewmembers on landing day within 4 h after long-duration space flight. One subject was able to perform and complete one trial of the FMT, while the other two were not able to perform the task. Since there was available only one data point on the landing day session, this data point was not included as part of the analysis presented here. Post-flight FMT data were obtained for 4–6 sessions, the first of which was 1 day after landing, and the remaining tests ranging between 2 and 46 days after landing. Subjects typically performed six trials of the FMT per session. However, on the first post-flight session, one subject performed only one trial, and another performed only three trials. Two subjects did not perform the FMT even once on the first day after return from space flight.

FMT trial procedures

In each test session crewmembers were instructed to "walk as quickly and as safely as possible without running or touching any of the obstacles on the course". This task was performed three times in the clockwise direction and three times in the counterclockwise direction in a randomized order. Subjects were allowed to rest between trials, especially immediately after flight, and all six trials were completed within a 10-min window. To prevent injury from falling, in addition to the medium-density foam on the floor, subjects wore a harness while being monitored by a "spotter." The spotter walked near the subjects (especially post-flight), ready to grab them by the harness straps to ensure their safety during all phases of the experiment. After a verbal "ready" indication, subjects began to walk the course. The primary outcome studied was the time (in seconds) to complete the course (TCC), regardless of whether contact was or was not made with the obstacles.

Data analysis

Magnitude of dysfunction in FMT

Increases in TCC were assumed to reflect deficits in subjects' locomotor control following long-duration space flight. A preliminary analysis of pre-flight data indicated that each subsequent trial within each session was faster, thus suggesting a learning effect over trials. Therefore, for determining the magnitude of dysfunction and the recovery of function to pre-flight levels, only observations from the first trial of each session were used. However, for determining the motor learning effect data from all six trials from both the pre-flight and first post-flight sessions were used.

Recovery of FMT function after space flight

To assess the overall recovery of locomotor function after return from space flight, a multilevel exponential recovery model was fit to the log-transformed TCC data from the first trial of each post-flight session for each crewmember. The model was of the form

$$y_{ij} = \mu_i(t_{ij}) + e_{ij} \tag{1}$$

where

$$\mu_i(\mathrm{t}_{ij}) = \begin{cases} A_i & \text{pre-flight} \\ A_i + B_i \mathrm{e}^{-C_i t_{ij}} & \text{post-flight} \end{cases} \tag{2}$$

is the expected log TCC response for the ith astronaut on the first trial on the jth session occurring t_{ij} days after the ISS mission landing event. In this model, we assume that for post-flight sessions, $\mu_i(t)$ is greater than and follows an exponential recovery trend back to its pre-flight value over the recovery period (B_i, $Ci > 0$). Thus, larger values of C_i reflect a faster recovery. The term e_{ij} (Eq. 1) reflects random variation for the ith subject not directly attributable to t_{ij}. A detailed description of this exponential model and the methodology for estimating its parameters are described in the "Appendix".

Short-term learning

In order to assess the early motor learning responses after returning from space flight, we modeled performance over the six trails during the first post-flight session by the exponential relation

$$y_{ij} = D_{ij} \mathrm{e}^{-E(j-1)}. \tag{3}$$

In Eq. 3, y_{ij} is the TCC for the ith subject and jth trial in the first post-flight session, E_i characterizes the short-term learning rate, and D_{ij} is a normalizing constant that contains a random error term (see "Appendix" for details). As two subjects could not perform the FMT in the first post-flight session and one subject did so only once, data from only 15 subjects (one of whom only performed 3 trials) were used for this short-term recovery analysis.

Recent studies have shown that this short-term learning is affected during adaptations to novel sensorimotor rearrangements in different populations (Bock 2005; Pisella et al. 2004; Bock and Girgenrath 2006). To compare the rate of short-term learning during the first post-flight session with that of the last pre-flight session, we used another model similar to (3) for the combined data, except that this model contained a term to distinguish between pre- and post-flight sessions (see Eq. 10). The same 15 subjects were used for fitting this model as used in (3).

Results

Magnitude of dysfunction in FMT

Figure 2 shows the trend lines of first-trial TCC pre-flight and 1 day after return for the 16 subjects with data from both sessions. Throughout the sessions, subjects were usually able to avoid the obstacles. One subject failed to avoid obstacles twice in a session 1 day after return. In all other sessions, pre- and post-flight, subjects were able to completely avoid obstacles, or failed to avoid only once. All of our subjects completed the FMT task without falling. All crewmembers exhibit altered locomotor function after long-duration space flight, with a median 48% increase in the time to complete the FMT course.

Recovery of function in FMT

Figure 3 shows estimated values of the median, middle 50%, and middle 95% of the distribution of TCC for pre-flight sessions and as a function of time after landing for post-flight sessions, overlaid with a plot of actual log TCC values. The percentiles of the TCC distribution were obtained empirically by using the fitted model (1) to simulate data from 10,000 hypothetical "subjects" performing the FMT at the same time points as in the actual study. Figure 3 suggests that the model's trend and variability described the actual data quite well. Note that only seven of the total 103 data points (6.8%), and six of 83 (7.1%) post-flight data points fall outside of the 95% intervals. Two

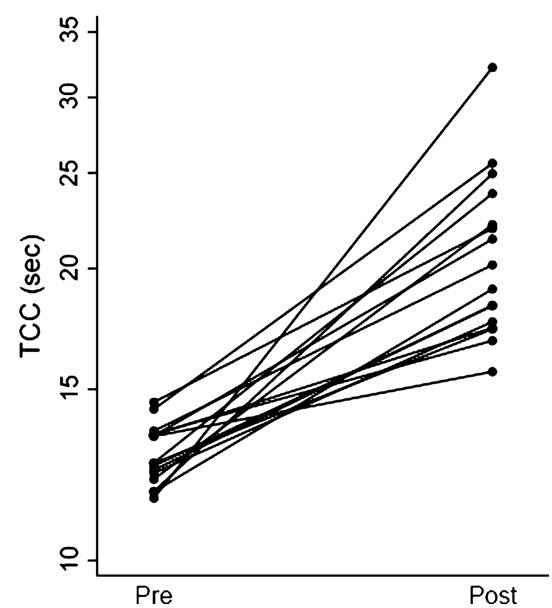

Fig. 2 Data of first-trial time to complete the course (TCC) pre-flight and 1 day after landing for 16 subjects. Two subjects did not perform the FMT 1 day after landing

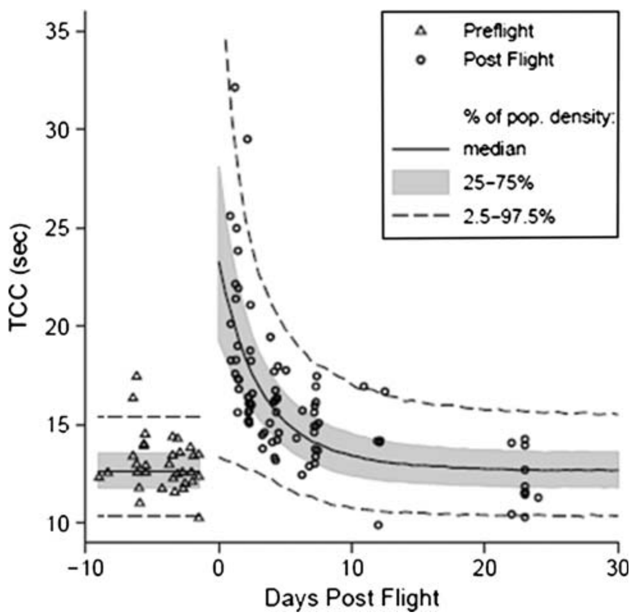

Fig. 3 A scatter plot of actual time to complete the course (TCC) values overlaid with TCC median, middle 50%, and middle 95% of the distribution as estimated by the multilevel exponential recovery model (constant for pre-flight and time-dependent for post-flight). Pre-flight times have been condensed for display purposes

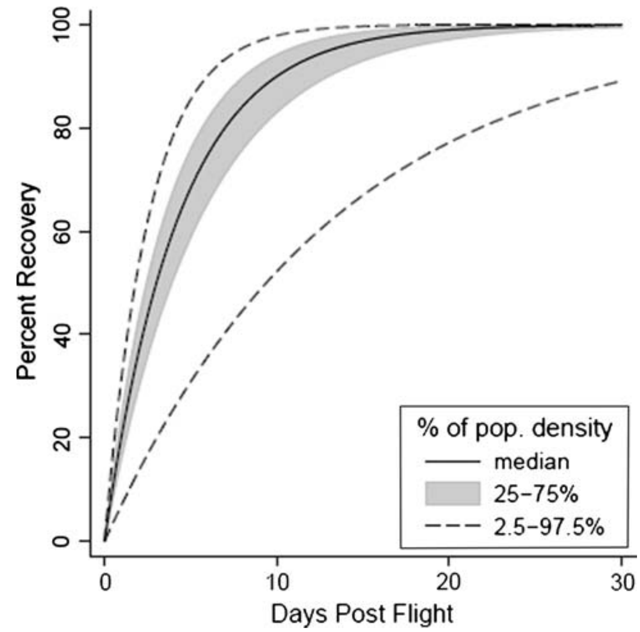

Fig. 4 Fraction of the population that would be expected to attain a certain percentage of recovery t days after landing. We expect that immediately post-flight most subjects would experience some deficit in performance resulting in increased FMT transit times relative to their pre-flight levels. We define percent recovery to be the percent of this (subject-specific) deficit that is made up over time. Thus, by definition, subjects are 0% recovered at $t = 0$, and are 100% recovered when their transit times reach preflight levels

subjects were excluded from consideration when estimating the covariance of the random effects parameters. For two subjects, original predicted values of the subject specific model parameters are such that they would violate the assumptions of the model. In these specific cases the model given by Eq. 1 would not make sense, since these subjects' expected TCC's would increase exponentially in sessions after landing. Examination of the raw data for these subjects revealed a slight increase in TCC after flight with no clear improvement trend; hence, an exponential recovery model could not be reliably fit to these data.

Figure 4 shows the fraction of the astronauts that would be expected to attain a certain percentage of recovery t days after landing. We expect that immediately post-flight most astronauts would experience some deficit in performance resulting in increased FMT transit times relative to their pre-flight levels. We define percent recovery to be the percent of this (subject-specific) deficit that is made up over time. Thus, by definition, subjects are 0% recovered at $t = 0$, and are 100% recovered when their transit times reach pre-flight levels. From the fitted model we calculated that a typical subject (solid line in middle of gray area) would recover to 95% of his/her pre-flight level at approximately 15 days post-flight.

Motor control strategies in recovery

Figure 5a shows a scatter plot of a single crewmember's TCC-values (s) for all trials on each session during the different days of post-flight testing. The horizontal line is the crewmember's average TCC for the last pre-flight session, while the dashed curve illustrates the fit to the first trial TCC across post-flight sessions using Eq. 2. This crewmember essentially recovered to his/her pre-flight level within 7 days. Note also that a distinct improvement in performance is seen over the trials *within* each day of testing. Figure 5b shows the exploded view of this person's TCC values both pre-flight and on 1 day after return from space flight, with separate fits to Eq. 3 (dashed curves). The mean short-term learning parameter (analogous to the mean of E_i in Eq. 3) was greater post-flight than pre-flight [$P = 0.042$, 95% confidence interval (0.00, 0.04), see Eq. 10].

We have recently shown that short-term learning and the long-term adaptive responses are related (Richards et al. 2007). From the present study, Fig. 6 shows the scatter plot of the subject-specific long-term recovery and short-term learning parameters (C_i and E_i, respectively) for the subjects used to fit both the model (Eq. 3) and the covariance structure of Eq. 2. To assess the sign and degree of association, we used Kendall's *Tau* (Gibbons and Chakraborti 2003), which is insensitive to nonlinearity and outliers. For these data, we found the association between the long-term recovery and short-term learning parameters (C_i and E_i,

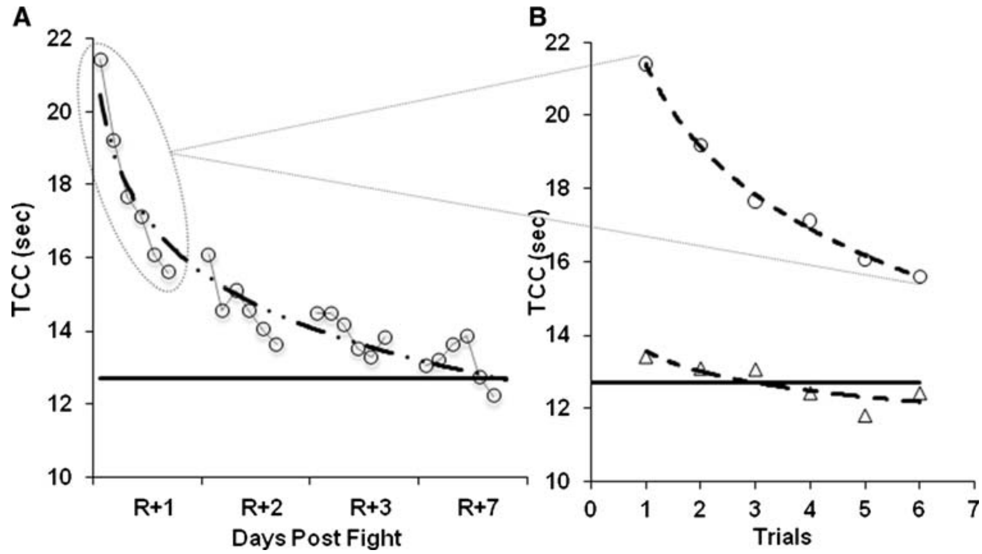

Fig. 5 **a** Scatter plot of a single crewmember's time to complete the course (TCC) values (in seconds) for all trials on each session during the different days of post-flight testing. The *dashed-dot curve* illustrates the fit to the first trial TCC across post-flight sessions using Eq. 2. **b** The exploded view of this person's TCC values across trials on the last pre-flight session (△) and on 1 day after return from space flight (○), with separate fits to Eq. 3 (*dashed curves*). In both panels, the horizontal line is the crewmember's average TCC for the last pre-flight session

respectively) to be significant and positively correlated [Kendall's $Tau = 0.69$, $P < 0.001$, 95% confidence interval (0.45, 0.92)].

Discussion

Magnitude of dysfunction and recovery of function in FMT

The goal of this study was to assess locomotor dysfunction and recovery of function after long-duration space flight using a functional task that consisted of traversing an obstacle-avoidance course. The results of the study indicated that over the 16 individual subjects who could complete the FMT 1 day post-flight, there was a median increase of 48% in TCC relative to pre-flight 1 day after their return. All subjects appeared to perform the FMT task by trading speed with obstacle avoidance or balance maintenance during the post-flight recovery period as compared to pre-flight. We estimated that the time for a typical subject to achieve 95% recovery of FMT performance after long-duration space flight would be approximately 15 days.

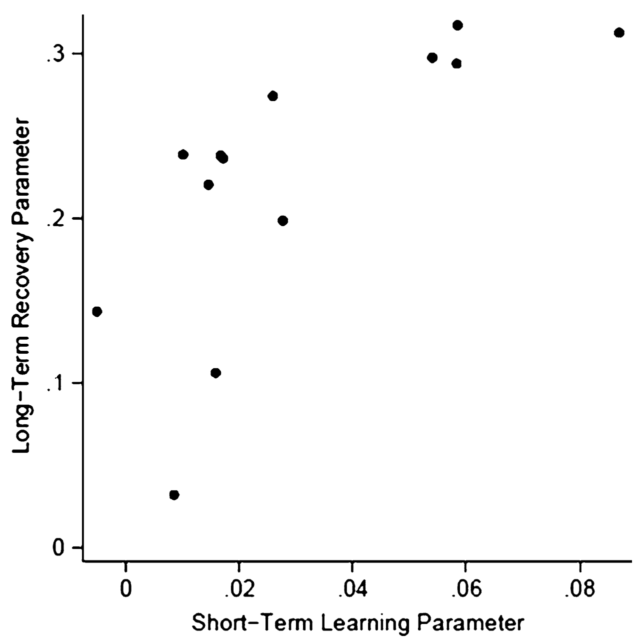

Fig. 6 Scatter plot of the subject-specific long- and short-term recovery parameters (C_i and E_i, respectively). Data show an association between long- and short-term recovery parameters

Locomotion is a complex task, demanding coordination of the eye–head, head–trunk and lower limb locomotor apparatus. Goal-directed locomotion, as was tested using the FMT, required subjects to trade off their walking speed with their ability to maintain equilibrium and coordination while negotiating the obstacles. Negotiating the obstacles on the course required modifying the heading direction to avoid hitting the pylons, bending at the waist or lowering themselves to avoid hitting the horizontal bar hung from the ceiling and stepping over obstacles and balancing on a single foot to step through the portal, and using equilibrium skills to maintain balance on the compliant surface. Further, walking on the foam surface increases the instability of the upper body as compared to a solid surface (Marigold and Patla 2005) and increases the reliance on vestibular derived information (Jeka et al. 2004). Reports on astronauts' responses during adaptation of illusory self motion and the simultaneous compensation for these motions when viewing a rotating display of dots on the inside of a rotating drum, or vertical optokinetic stimulation in microgravity suggest that reliance on visual cues is increased and on graviceptor signals is reduced (Mueller et al. 1992, 1994; Oman et al. 1986, 2000; Reschke et al. 1998; Watt et al.

1993; Young et al. 1984; Young and Shelhamer 1990). In some astronauts local tactile cues from bungee cord-induced foot pressure inhibited visually induced motion illusions (Young et al. 1992). More recent work has shown that astronauts in microgravity become more dependent on dynamic visual and proprioceptive cues as well as static visual orientation cues (Oman et al. 2000). These illusions of self motion continue to be reported during reentry and immediately after landing in response to voluntary pitch or roll head movements or passive roll stimulation in darkness immediately after landing (Reschke and Parker 1987; Young et al. 1984). Adaptation to microgravity results in lack of bipedal balance control under post-flight test conditions requiring accurate feedback from the vestibular inputs and ankle proprioception on computerized dynamic posturography (Paloski et al. 1992, 1994; Paloski 1998). Most of the subjects had increased reliance on feedback from vision during their recovery process as a result of degraded performance of the other two feedback systems during adaptation to microgravity (Reschke et al. 1998). Proprioceptive function also adapts to microgravity, as reported by Roll et al. (1993, 1998), causing the reduction in relevance and coding of proprioceptive inputs during standing posture and body movements, and enhanced reports of movement illusions in response to tendon vibrations (Reschke et al. 1998; Roll et al. 1993, 1998). Therefore, adaptation to microgravity causes a different combination of reliance on visual, proprioceptive and vestibular cues underlying sensorimotor processing of body orientation and posture post-flight. Also, previous work has shown that after space flight astronauts experienced sensorimotor changes indicated by changes in spinal circuitry function: altered H, otolith-spinal and stretch reflex characteristics (Reschke et al. 1986; Watt et al. 1986; Harris et al. 1997), modifications in proprioceptive functioning (Kozlovskaya et al. 1981; Watt et al. 1985), and loss in muscle strength and tone (Fitts et al. 2000). All of these changes may have contributed to the change in subjects' post-flight FMT performance.

The recovery of physiological function after space flight has been measured in several systems individually, showing a wide range of recovery times. Studies show otolith receptors recovering after a day (Boyle et al. 2001), the neuromuscular complex recovering in 1–3 weeks (Edgerton and Roy 1996; Antonutto et al. 1999), and bone tissues taking up to several months (Vico et al. 2000; Sibonga et al. 2007). In a study Courtine and Pozzo (2004) reported that near optimal locomotor abilities were restored in subjects when they were tested on complex tasks on the sixth day after their return from long-duration space flight. This difference from our findings in the present study may be due to differences in the task requirements of the two tests.

Motor control strategies in recovery

The results of the present study also show that post-flight recovery can be divided into two processes: rapid strategic learning over the six trials on the first day after return, and a slower process taking over 2 weeks to recover to a pre-flight level of functional performance. The individual subjects' short-term learning parameters over the first post-flight trials and their long-term recovery parameters across sessions were significantly positively associated. Several studies have examined the time course of motor learning in different training paradigms such as a visual discrimination task (Karni and Sagi 1993, for review see Karni and Bertini 1997) or while learning to adapt to distortions either visual (Redding and Wallace) or mechanical (Shadmehr and Mussa-Ivaldi 1994; Kording et al. 2007). The time course of motor learning has been described to occur in two stages: (1) a fast, within-session improvement that can be induced by a limited number of trials on a time scale of minutes and (2) a slowly evolving, incremental performance gain, triggered by practice but taking hours to become effective (Karni and Bertini 1997). These two learning processes for motor adaptation to sensory discordances have also been described as strategic control versus adaptive realignment (referred to as "adaptation"), respectively (Redding and Wallace 1996; Clower and Boussaoud 2000; Bock 2005). In support of the concept that two processes control adaptation, recent studies have shown that motor adaptation is driven by two distinct neural systems that differ from each other in terms of their sensitivity to error and their rates of retention (Smith et al. 2006). Separate neural substrates have also been shown to control the execution of these two motor strategies (Pisella et al. 2004; Luauté et al. 2009). Pisella et al. (2004) reported that a patient with a bilateral lesion of the posterior parietal cortex (PPC) was not able to implement on-line strategic adjustments in response to a prismatic shift in visual feedback during a pointing task, yet showed adaptive after-effects. The authors contended that the strategic component was linked to the posterior parietal cortex, and the adaptive component was linked to the cerebellum. Anguera et al. (2010) have further showed that cognitive processes such as spatial working memory contributed to the early and not the late stage of motor learning by comparing the rates of adaptation and overlap of the neural substrates of this cognitive and the two motor learning stages during a visuomotor adaptation task. Thus, we contend that these two distinct motor learning stages can influence the rate of post-flight recovery while readapting to Earth's gravity.

Strategic perceptual-motor control occurs early in the adaptation process once the subject becomes aware of the sensory manipulation and understands on some conscious level how to correct for it (Redding and Wallace 1996; McNay and Willingham 1998; Seidler 2004). For example, subjects exposed to a prismatic lateral shift in vision make strategic corrections in pointing movements based on visual feedback to improve performance and eventually point directly to a target (Weiner et al. 1983; Rossetti et al. 1993; Welch et al. 1993). Many of the changes observed during locomotion immediately after space flight represent strategic responses. As shown in Fig. 5, there was distinct improvement in performance within each day and across the post-flight testing sessions. We infer that the short-term trend represents rapid strategic learning, and the long-term trend represents adaptive remodeling. This early learning may be achieved by involving strategic processes that reorganize motor responses to produce an optimized solution enabling terrestrial locomotion during a period of intense sensorimotor adaptive flux while recalibrating to Earth's 1-g environment (Bloomberg and Mulavara 2003). Strategic control is important for improving performance when first encountering a new visuo-motor discordance (Bock 2005), is task-specific, and does not generalize to other visuo-motor discordances (Redding and Wallace 1996; McNay and Willingham 1998). Repeated, multiple exposures to the visuo-motor discordance are required to reinforce strategic sensorimotor coordination patterns until they become more automatic, and therefore adaptive, in nature (Weiner et al. 1983; Redding and Wallace 1996). We infer that the long-term trend represents adaptive remodeling.

Redding and Wallace (2002) suggested that adaptation to a visuo-motor discordance involves a dynamic interplay between strategic corrections and adaptive realignment, with both developing simultaneously and interacting with each other. We recently demonstrated this dynamic interplay by showing that subjects display a gradual reduction in the strategic modification of trunk movements during exposure to varied optic flow during treadmill walking. Importantly, the rate at which strategic control is reduced is related to the magnitude of post-exposure adaptive responses in locomotor control (Richards et al. 2007). Results from the present study show that subjects who demonstrated a fast initial learning effect 1 day after landing also show a faster overall recovery during the post-flight recovery period. This indicates that the rapid and long-term recovery rates are related, suggesting an interplay between the underlying motor learning mechanisms. In an experiment to study the relationship between implicit and explicit processes during motor learning in an adaptive realignment experiment of visuomotor rotation in a pointing task, it was found that opposing strategies cannot substitute for adaptive realignment imposed during the performance of the task (Mazzoni and Krakauer 2006). However, this may occur due to strategic and adaptive responses having opposing goals while they may be congruous in our study. Bock and Girgenrath (2006) investigated the strategic and adaptive realignment components of sensorimotor adaptation in young and elderly subjects. They found that the recalibration processes in the elderly subjects were not impaired compared to the young subjects, as shown by the magnitude of after effects and transfer of adaptation to novel sensorimotor arrangements. However, they have shown that the strategic processes as represented by improvements during exposure are degraded in the elderly (Bock 2005; Bock and Girgenrath 2006).

Therefore, two types of recovery processes interact with each other and influence an astronaut's ability to re-adapt to Earth's gravity environment. Initial strategic modifications help astronauts make rapid modifications in their motor control strategies emphasizing error reduction (Redding and Wallace 2002). This type of recovery may be critical during the first hours after landing. These strategic processes may influence the adaptive realignment process that enables long-term plastic recalibrations to occur that perhaps involve morphological and synaptic changes. Thus, strategic processes serve to reinforce the adaptive realignment processes facilitating re-adaptation to Earth's 1-g environment on return from space flight. Gait adaptability training programs currently being developed to facilitate adaptive transition to planetary environments can be optimized to engage both strategic and plastic processes to facilitate rapid restoration of post-flight functional mobility.

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Appendix

Long-term recovery model

For the model in (1), $\mu_i(t_{ij})$ is the expected log TCC response for the ith astronaut on the first trial on the jth session occurring t_{ij} days after the ISS mission landing event. For pre-flight sessions, t_{ij} is defined as the negative of days prior to lift-off ($t < 0.$). We assume that for post-flight ($t > 0$) sessions, $\mu_i(t)$ is greater than $\mu_i(t < 0)$, and that for $t > 0$, $\mu_i(t)$ follows an exponential recovery trend back to $\mu_i(t < 0)$ as t increases. Earlier we defined $\mu_i(t_{ij})$ as

$$u_i(\mathrm{t}_{ij}) = \begin{cases} A_i & \text{pre-flight} \\ A_i + B_i \mathrm{e}^{-C_i t_{ij}} & \text{post-flight} \end{cases}.$$

For statistical analysis we break down Ai, B_i, and C_i into fixed and random components as

$$\begin{aligned} A_i &= \beta_0 + u_{0i} \\ B_i &= \beta_1 + u_{1i}\,. \\ C_i &= \theta + u_{2i} \end{aligned}$$

Thus,

$$\mu_i(t_{ij}) = \begin{cases} \beta_0 + u_{0i} & \text{pre-flight} \\ \beta_0 + u_{0i} + (\beta_1 + u_{1i})\exp\left(-(\theta + u_{2i})t_{ij}\right) & \text{post-flight} \end{cases}. \tag{4}$$

The parameter β_0 is the population expected pre-flight value of log TCC, and u_{0i}, u_{1i}, and u_{2i} are subject-specific random effects with the vector $\boldsymbol{u} = (u_{0i}, u_{1i}, u_{2i})'$ assumed to follow a multivariate normal distribution with mean 0 and covariance matrix $\boldsymbol{V}$. The quantity $\beta_1 + u_{1i}$ represents the expected change in log TCC for the ith subject on landing day, and $\theta + u_{2i}$ is the ith subject's long-term recovery parameter (over days), the exponential constant that determines the speed of the recovery process (larger values of $\theta + u_{2i}$ are consistent with faster recovery).

Estimating model parameters

Let $\hat{\theta}$ be the maximum-likelihood estimate of θ, and let $\hat{\mu}_i(t_{ij})$ be (Eq. 4) with $\theta = \hat{\theta}$ fixed. With fixed $t_{ij} > 0$ (post-flight) and varying u_{2i}, we can consider $\mu_i(t_{ij})$ as a function of u_{2i} and expand $\exp(–u_{2i}t_{ij})$ around $u_{2i} = 0$ to give

$$\begin{aligned} \hat{\mu}_i(t_{ij}) &\doteq \beta_0 + u_{0i} + (\beta_1 + u_{1i})\exp(-\hat{\theta}t_{ij}) + u'_{2i}t_{ij}\exp(-\hat{\theta}t_{ij}). \\ &\doteq \beta_0 + u_{0i} + (\beta_1 + u_{1i})X_1 + u'_{2i}X_2 \end{aligned} \tag{5}$$

where

$$\begin{aligned} u'_{2i} &= -(\beta_1 + u_{1i})u_{2i}, \\ X_1 &= \exp(-\hat{\theta}t_{ij}), \\ X_2 &= t_{ij}\mathrm{X}_1. \end{aligned} \tag{6}$$

By fitting a linear multilevel model to y_{ij} with X_1 and X_2 as explanatory variables in both the fixed and random parts of the model, one obtains regression coefficients b_0, b_1, and b_2 corresponding to the constant, X_1 and X_2 in the fixed part of the model. From Eq. 5, it can be seen that b_0 and b_1 are estimates of β_0 and β_1, respectively, while b_2 is an estimate of $E(u'_{2i}) = –\mathrm{Cov}(u_{1i}, u'_{2i})$ In addition, best linear unbiased predictors (BLUPs) of u_{0i}, u_{1i}, and u'_{2i} can be obtained. From the latter two of these, we can get a prediction of u_{2i} using Eq. 6:

$$\hat{u}_{2i} = \frac{-\hat{u}'_{2i}}{b_1 + \hat{u}_{1i}}, \tag{7}$$

where $\hat{u}_{1i}$ and $\hat{u}'_{2i}$ are BLUPs of u_{1i} and u'_{2i}, respectively, and from these estimates we calculate $C_i = \theta + u_i$.

We determined the maximum-likelihood estimate $\hat{\theta}$ using the profile-likelihood method. Under this method, trial values of $\hat{\theta}$ are substituted in the linearized model (Eq. 5). For each trial value, the model is then fit with respect to all other parameters, and the conditional likelihood is recorded. The value of θ which maximizes the conditional model likelihood is taken to be the maximum-likelihood estimate, $\hat{\theta}$, and the final estimates for the parameters are those obtained using this value of $\hat{\theta}$.

Short-term learning model

Let $z_{ij} = \log(y_{ij})$. Then the equation (3)

$$y_{ij} = D_{ij}\, e^{-E(j-1)}.$$

is equivalent to

$$z_{ij} = D'_i - E_i(j-1) + e'_{ij} \tag{8}$$

with $D_{ij} = \exp(D'_i + e'_{ij})$. We again break these coefficients into fixed and random effects,

$$\begin{aligned} D'_i &= \alpha_0 + \upsilon_{0i} \\ E_i &= \alpha_1 + \upsilon_{1i}, \end{aligned}$$

so the model for short-term learning is

$$Z_{ij} = (\alpha_0 + \upsilon_{0i}) - (\alpha_1 + \upsilon_{1i})(j-1) + e'_{ij}. \tag{9}$$

Here, α_0 and α_1 are fixed parameters, υ_{0i} and υ_{1i} are random effects having a bivariate normal distribution, and e'_{ij} is an independent, normally distributed, within-subject error term. The coefficient $\alpha_1 + \upsilon_{1i}$ (which should be positive) quantifies how quickly subjects can improve performance, trial-by-trial, during the day of testing. Larger values imply faster adaptation. Best linear unbiased predictors were used to calculate E_i.

Pre- versus post-flight learning comparison model

We used another mixed effects regression model similar to Eq. 9 for comparing the mean rate of improvement in performance during the last pre-flight session with rate of improvement during the first day after return:

$$z_{ij} = \begin{cases} (\varphi_0 + b_{0i}) + (\varphi_1 + b_{1i})(j-1) + e''_{ij} & \text{pre-flight} \\ (\varphi_0 + b_{0i}) + (\varphi_1 + b_{1i})(j-1) \\ \quad + (\varphi_2 + b_{2i}) + (\varphi_3 + b_{3i})(j-1) + e''_{ij} & \text{post-flight} \end{cases} \tag{10}$$

The same 15 subjects were used for fitting this regression model as used for calculating BLUPs of v_{1i}'s in Eq. 9.

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